

DEFENDED FORTRESSES OR MOVING TARGETS? ANOTHER MODEL OF INDUCIBLE DEFENSES INSPIRED BY MILITARY METAPHORS

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Abstract.—We use a common framework to compare three models of plant strategies to confront herbivory: constitutive defense, optimal inducible defense, and the “moving target.” Plants with constitutive defenses retain a fixed defensive phenotype. Plants with optimal inducible defenses respond to attack by increasing defenses. Plants following the moving target strategy respond to attack by altering phenotype. The constitutive and optimal inducible defense models, unlike the moving target model, require that plant phenotypes can be arrayed along an axis representing the trade-off between cost and defense. We argue that the evidence for such an axis is not yet convincing. Our models indicate that constitutive defenses are favored when herbivory is relatively constant or when multiple herbivores attack and costs of defense or defensive machinery are high. Optimal inducible defenses are favored when herbivory rates vary, costs are not too high, and plant phenotypes can be arrayed along a defense axis. The moving target strategy is favored when costs are not too high, herbivory rates vary, and plant phenotypes effective against one herbivore are ineffective against others. We conclude that the moving target strategy might be a robust response to unpredictable and uninformative environments.

Resistance of plants against herbivores is often observed as a transient trait rather than one that is constantly expressed in a given host plant (Rhoades 1979; Karban and Myers 1989; Tallamy and Raupp 1991). Many experiments have shown that resistance can be induced by the attacks of herbivores, but almost all researchers note considerable variability in the effects of plant responses on herbivore performance (Coleman and Jones 1991; Faeth 1991). Damage by herbivores can make a plant more resistant, have no effect, or make the plant more susceptible to subsequent attacks (Myers and Williams 1984; Fowler and Lawton 1985; Haukioja 1990).

If plants can produce effective defenses, why do we observe so many plant species that have inducible rather than constitutive (fixed) defenses? Many recent workers have asked this question both informally (Rhoades 1979; Harvell 1986, 1990a; Matson and Hain 1987; Karban and Myers 1989; Baldwin et al. 1990; Karban 1993b) and formally (Lively 1986; Edelman-Keshet and Rausher 1989; Riessen 1992). Common elements thought to favor inducibility are that defenses

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TABLE 1
BASIC PROPERTIES OF THE THREE MODELS

Property	Constitutive Defense	Optimal Inducible Defense	Moving Target
Individual phenotype	Fixed	Variable	Variable
Response to attack	None	Defend	Change
Response to no attack	None	Un-defend	None
Cost of "defense"	Yes	Yes	No
Effectiveness of defense	Yes	Yes	Usually yes

are costly and that levels of herbivory are variable over time. In these circumstances, selection favors inducible resistance because the plant can save defense costs when herbivores are absent. Our goal in this article is to compare the circumstances favoring the constitutive defense and inducible defense strategies with an alternative form of inducible response we call the "moving target" strategy.

Table 1 and figure 1 present the basic assumptions of the models to be compared in this article: the constitutive defense model, the optimal inducible defense model, and the moving target model. The constitutive defense model describes a population of plants each of fixed defensive phenotype. Any polymorphism in such a population must be genetic. The optimal inducible defense model describes a population of plants each of which responds to attack by increasing defenses and responds to the absence of attack by decreasing defenses. Polymorphism in such a population need have no genetic component (Adler and Harvell 1990). The moving target model describes a population of plants each of which responds to attack by altering phenotype and does not change in the absence of attack. The constitutive and inducible defense models are similar in that the population of plants can be arrayed along an axis of more to less defended, with defended plants suffering less herbivory in the presence of herbivores at the price of the cost of defense. The axis might represent the concentration of a particular secondary metabolite. The moving target model assumes no such axis of defense phenotypes. In its most basic form, each phenotype has the same intrinsic growth rate and competitive ability and is relatively susceptible to some herbivore.

In the following section we argue that the evidence for costs and directional responses is not yet convincing. This article presents quantitative versions of alternative verbal models for induced resistance to herbivores (Karban and Myers 1989; Karban 1993*b*). We wish to challenge the intuition that saving unnecessary costs has driven the evolution of inducible responses and argue that inducible responses may be favored even if costs of defense are negligible and description of responses as defenses is inappropriate. The moving target model describes induced responses to herbivory that are a form of nondirectional phenotypic escape from bad conditions rather than a beefing up of defense. The strategy resembles dispersal from unfavorable habitat in that an individual plant can attempt to evade bad conditions (herbivory) by running away (changing phenotype).

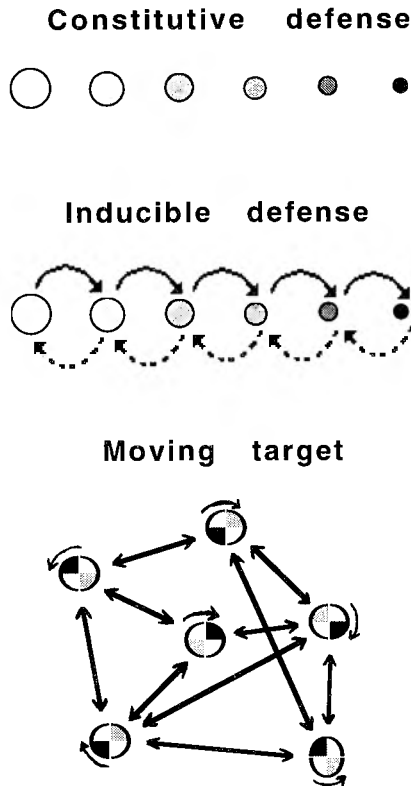


FIG. 1.—Comparison of the constitutive, optimal inducible, and moving target strategies. Each dot represents a different plant phenotypic state, with dot size showing growth rate in the absence of herbivory and dot shading showing degree of resistance. Solid arrows depict switching in response to herbivory; dashed arrows depict switching in response to the absence of herbivory. The twirling, variegated dots in the illustration of the moving target strategy indicate that resistance is an unpredictable function of time, history, and the herbivore regime.

Of course, responses may be regulated, but a great number of factors (plant genotype, plant age, plant state, the type of herbivory, etc.) influence them. From the herbivore's point of view, these factors can give the impression of randomness. Plant phenotypes cannot be arrayed along a single axis from undefended to defended in this model because a plant's response consists of a great variety of chemical changes, each of which is differentially affected by environmental conditions, and each of which has some independent component of effect on herbivores. Finally, change may or may not be effective as a defense. Just as a disperser might leave a bad situation only to arrive somewhere worse, a moving target might switch from a heavily attacked phenotype to one proving even more vulnerable. When an organism leaves a state that is worse than average, however, it will, on the average, find itself better off.

This trade-off between the effectiveness of different phenotypes requires that

some herbivores do poorly on some plant phenotypes and well on others. We present evidence in the following section that this may be the case. Plants will not fix their phenotype in a state resistant to one set of herbivores if that state is vulnerable to attack by a different set. Plants using the moving target strategy benefit in ecological time; the herbivory they escape would be their own. The attacking herbivores and their immediate progeny have decreased effectiveness rather than decreased ability to evolutionarily track their host plant (as proposed by Whitham et al. [1984]; Harvell [1990b]).

In this article, we present formal models of constitutive resistance, optimal induced resistance, and the moving target. By presenting the models in a single framework, we can effectively contrast their assumptions. We use the models to predict the dynamics of plant defenses and plant biomass when faced by a variety of herbivory regimes, seeking the conditions favoring each strategy.

THE ASSUMPTIONS

The key distinctions between defense models and the moving target model hinge on whether the different plant phenotypes can be meaningfully characterized as defenses—in particular, whether phenotypes can be arrayed along a single axis from most susceptible and least costly to least susceptible and most costly. We review studies of cost in inducible plants, effects of plant phenotypes on multiple herbivore types, and plant response to argue that several aspects of the defense model are not strongly supported by existing data.

Several studies have measured costs in inducible plants by comparing correlates of fitness, in the absence of herbivory, between plants that had and had not been induced. Injections of chitin were used to induce the production of proteinase inhibitors in cultivated tomato plants (Brown 1988). High induced concentrations of proteinase inhibitors were not associated with any reduction in plant growth or reproduction. In another study, concentrations of alkaloids were induced in wild tobacco plants (Baldwin 1988). Total mass of induced plants was reduced by about 15%, and the number of fruits per plant was reduced by 38% (Baldwin et al. 1990). Surprisingly, seedlings that were induced maintained high concentrations of alkaloids throughout their lives rather than reverting to a less defended and presumably less costly state (I. Baldwin, personal communication). In a third study, resistance in wild cotton plants was induced by early-season feeding by caterpillars (Karban 1993*a*, 1993*b*). The induced plants supported fewer caterpillars than the noninduced controls throughout the rest of the season but suffered no measurable decrease in growth or seed production in the absence of herbivory.

The evidence to date does not provide strong support for the assumption that induced resistance against herbivores has a measurable fitness cost. Indeed, the evidence for costs of phenotypic plasticity in general remains weak (Sultan 1992). This need not imply that costs are negligible, because costs are very difficult to measure empirically. Small but consistent costs below the detection threshold of existing analytical techniques could be sufficient to direct the course of evolution (Simms 1992; Karban 1993*b*).

Other studies have compared the effects of inducible responses on different herbivores, finding, somewhat counterintuitively, highly herbivore-specific effects. For example, damaged squash leaves became more vulnerable to one and more resistant to another species of beetle naturally co-occurring with the plant in southeastern Mexico (Carroll and Hoffman 1980). This strong dichotomy of effect has been found recently for many other beetle species feeding on other cucurbits (Tallamy and McCloud 1991). In another well-studied system, divergent effects of damage have been reported for the herbivores of birch. Artificial damage to birch leaves retarded the development of four species of caterpillars and two species of sawflies, although for two other sawfly species development was unaffected or even accelerated relative to controls (Haukioja and Niemela 1979). In a second study of different herbivores on birch (Fowler and MacGarvin 1986), damage reduced numbers of geometrid caterpillars, phloem feeders, and weevils, although without reducing subsequent damage to the plant. However, damage by a species of case-bearing caterpillar was significantly increased on previously damaged branches. Bark beetles and their fungal associates that attack conifers represent another well-studied system. Monoterpenes that are induced during the attack have very different effects on different species of beetles (Raffa and Berryman 1987). Many other examples could be adduced of induced responses that have extremely different effects on different herbivores.

Not only do herbivores respond very differently to induced responses, but plant responses themselves have been found to vary considerably depending on subtle features of the abiotic and chemical environment of the plant tissue. For example, damaged solanaceous plants induce higher levels of oxidative enzymes that can have strong negative effects on herbivores (Duffey and Felton 1989). Effects of this induced response depend critically on the levels of plant protein available to the herbivore and the interaction of the induced oxidative enzymes with other plant processes. Oxidative enzymes can completely inactivate the effects of induced proteinase inhibitors in solanaceous plants. Induction of several different oxidative enzymes depends on the type and intensity of damage and the specific plant tissue that is damaged (Duffey and Felton 1989). Similarly, the effects of increasing the concentration of any particular antioxidant on cabbage loopers were found to increase or decrease the overall resistance depending on the presence and ratios of other antioxidants (Gonzalez-Coloma et al. 1990).

With this evidence, we think it worthwhile to present models that do not focus on costs, that include multiple herbivores with different responses to plant phenotype, and that follow phenotypic changes that cannot be predicted from plant species identity alone.

THE MODELS

Our model focuses on plants competing in a small region, besieged by herbivores with dynamics generated from a much larger region. The herbivore population dynamics are therefore unaffected by the status of the plant population. We here assume also that herbivore foraging behavior is unresponsive to the state

of the plant population. The Appendix presents models with behaviorally and numerically responsive herbivores.

Consider first a single species of plant (we use the terms *species* and *strategy* interchangeably). Such a plant can be in one of several phenotypic states, designated by i for $i = 1, \dots, n$. The parameters and variables are as follows: n , number of phenotypic states; i , index for phenotypic states; x_i , biomass of plants of state i ; \bar{x} , total biomass of plants; f , function describing competitive density dependence; r_i , intrinsic growth rate of plants of state i ; a_i , competitive sensitivity of plants of state i ; e_i , rate at which plants of state i are eaten; s_{ij} , rate at which plants switch from state i to state j ; and γ , proportionality constant in switching rates. We follow the biomass of plants in each state. The basic model is

$$\frac{dx_i}{dt} = r_i x_i - a_i f(\bar{x}) x_i - e_i x_i - \left(\sum_{j=1}^n s_{ij} \right) x_i + \sum_{j=1}^n s_{ji} x_j. \quad (1)$$

The first two terms represent density-independent and density-dependent growth, respectively, either of which could depend on state. To represent competition, f must be an increasing function of the total plant biomass density \bar{x} . The next term represents herbivory, where e_i gives the herbivory per unit biomass for a plant in state i and is expected to be very much a function of time. The first sum represents the rate at which plants switch from state i , summed over all possible switches to other states j . The switching rate will generally be a function of the success of the plant in state i . The second sum represents all plants switching into state i , summed over all other states j .

As noted above, the dynamics of the herbivores are imposed from without in the basic model. Parameters and variables for the herbivore submodel are m , number of herbivore types; l , index for herbivore types; h_l , biomass of herbivores of type l ; and k_{li} , ability of herbivores of type l to eat a plant in state i . We consider m herbivore types (possibly species or ecotypes), indexed by l , and denote the population of type l by h_l , a function of time. The coupling between the herbivore dynamics and the plant dynamics comes through the eating rate e_i , which is assumed to take the additive form

$$e_i = \sum_{l=1}^m k_{li} h_l. \quad (2)$$

The parameter k_{li} gives the rate at which herbivores of type l consume plants in state i . This could include some component of the relative apparency of plants in different states to the various herbivores but cannot include the effects of adaptive foraging strategies. The more complex models in the Appendix indicate how this can be done.

We next present the rules governing the constitutive, moving target, and optimal inducible strategies. Each is described by a different set of assumptions about the key parameters r_i , s_{ij} , and k_{li} .

The Constitutive Defense Model

A constitutively defended plant is characterized by $s_{ij} = 0$ (no switching). In this case, one can generally order the states from least to most defended, with the most defended states having the lowest average values of e_i and suffering the least herbivory. If costs of defense reduce the density-independent growth rate, r_i will be lowest for the most defended types. If costs of defense reduce competitive ability, a_i will be highest for the most defended types.

The Moving Target Model

The moving target strategy is characterized by

$$s_{ij} = \gamma e_i / n. \quad (3)$$

With this strategy, a plant switches from a state at a rate proportional to the rate at which it is getting eaten and chooses uniformly among states to which to switch. Note that detailed mechanisms depending on the many parameters describing a given plant (age, history, environment, etc.) could deterministically produce a rule indistinguishable from this rule from the perspective of an attacking herbivore. More sophisticated and potentially superior rules taking into account differences in growth rate among states could be devised. Our idea here is to illustrate the effectiveness of undirected change cued only by attack.

The Optimal Inducible Defense Model

We now derive the switching rule for the optimal inducible response to variation of a single herbivore population over time. A plant with such a strategy evaluates the fitness of the various states as a function of herbivory and switches to the state with the highest instantaneous growth rate in the presence of that herbivore.

When faced by only one herbivore type, the eating rate a plant experiences in a particular state is sufficient information to estimate the population size of the herbivores, the eating rate in any other given state, and thus its growth rate when in that state. Designating the single herbivore type by h_1 , we find that the eating rate experienced by a plant in state i is (from eq. [2])

$$e_i = k_{1i} h_1.$$

The herbivore population size can then be estimated as

$$h_1 = \frac{e_i}{k_{1i}},$$

from which the eating rate e_j experienced by a plant in state j can be computed to be

$$e_j = k_{1j} h_1 = k_{1j} \frac{e_i}{k_{1i}}.$$

We define g_i to be the growth rate of state i at a particular herbivore level, so that

$$g_i = r_i - e_i - a_i f(\bar{x}).$$

The growth rate g_j in the potential target state j has thus been estimated as

$$\begin{aligned} g_j &= r_j - e_j - a_j f(\bar{x}) \\ &= r_j - k_{1j} \frac{e_i}{k_{1i}} - a_j f(\bar{x}). \end{aligned}$$

The globally optimal inducible type switches immediately to the best state. In order to limit the switching rate and facilitate comparison with the moving target strategy, we set

$$s_{ij} = \begin{cases} \gamma(g_j - g_i) & \text{if } g_j \geq g_i \\ 0 & \text{if } g_j < g_i \end{cases} \quad (4)$$

and term this the optimal inducible type.

Any state with both low growth (low r_i or high a_i) and a low level of defense (high k_{1i}) will never be selected by this strategy. The remaining states among which this strategy chooses are thus necessarily characterized by trade-offs between defense and growth. Optimal inducible switching among these states is directional in that plants switch to more defended states with lower growth in the presence of herbivores and to less defended states with higher growth in their absence.

This strategy is optimal only in response to one particular herbivore and may be highly inappropriate for other herbivores or selective pressures.

FIXED HERBIVORE POPULATION SIZES

The type and magnitude of herbivore variability over time determines which of the above strategies is favored. We first show that switching can never be favored when herbivory is constant. The argument is simple: in the absence of environmental variation there is a best fixed state, and the constitutively defended individuals with that state cannot be outcompeted.

More explicitly, let x_i^* denote the equilibrium biomass of a constitutive species in state i . That is, x_i^* satisfies

$$r_i - e_i - a_i f(x_i^*) = 0.$$

Consider the state i^* with the maximal value of x_i^* . Then

$$x_{i^*}^* \geq x_j^*,$$

and, because f is an increasing function,

$$f(x_{i^*}^*) \geq f(x_j^*) \quad (5)$$

for every other state j . The growth rate of a potential invader in state j satisfies

$$r_j - e_j - a_j f(x_{i^*}^*) \leq r_j - e_j - a_j f(x_j^*) = 0.$$

Because an invasion is possible only when this growth rate is positive, no fixed type can invade the type i^* .

Suppose now that a general strategy, with switching, is attempting to invade a world saturated with constitutive individuals in state i^* . Denoting the biomass of invaders in state i by y_i , we have initially that

$$\frac{dy_i}{dt} = r_i y_i - a_i f(x_{i^*}^*) y_i - e_i y_i - \sum_{j=1}^n s_{ij} x_i + \sum_{j=1}^n s_{ji} x_j.$$

If \bar{y} represents the total biomass of this species, we find that

$$\frac{d\bar{y}}{dt} = \sum_{i=1}^n (r_i - a_i f(x_{i^*}^*) - e_i) y_i \leq 0$$

from equation (5). This expression is equal to zero only if all the invaders are in state i^* . Any strategy that includes any switching out of state i^* cannot invade.

In a fixed environment of this sort, many different strategies could express the same best phenotype, fixation of all plants in state i^* . The ability to switch might never be revealed without environmental variation. For example, an optimal inducible type faced by a single herbivore would express the same phenotype as a constitutive type. Constitutive plants would all be in state i^* because those individuals in other states had lost out in competition. Inducible plants would all be in state i^* because those individuals that started out in different states would have rapidly switched to i^* and never switched again. Plants following the moving target will switch out of state i^* and suffer as a consequence. In a fixed environment, the "bullets" are stationary and a moving target runs into them.

Figure 2 illustrates the results of competition of the three strategies when faced by an unchanging herbivory regime. The optimal inducible and constitutive strategies persist at equilibrium as soon as all individuals fix in the optimal state, while the moving target strategy is rapidly eliminated. The optimal inducible strategy ends up with more biomass than the constitutive strategy because of the initial conditions. Each strategy begins with equal biomass in each of two states. The inducible individuals in the inferior state rapidly switch to the superior state, while the constitutive individuals in the inferior state are defeated in competition, which explains the factor of two difference in the equilibrium biomass.

In a static world, one expects no phenotypic variability. If the herbivory environment varied spatially, multiple states might be maintained in the form of a cline, but individuals would have no incentive to switch once they had found the optimal state. Dispersal in such an environment could favor switching between generations.

VARIABLE HERBIVORE POPULATION SIZES

Herbivory levels, particularly those experienced by a single plant, are not constant. In this section, we compete the constitutive, optimal inducible, and moving

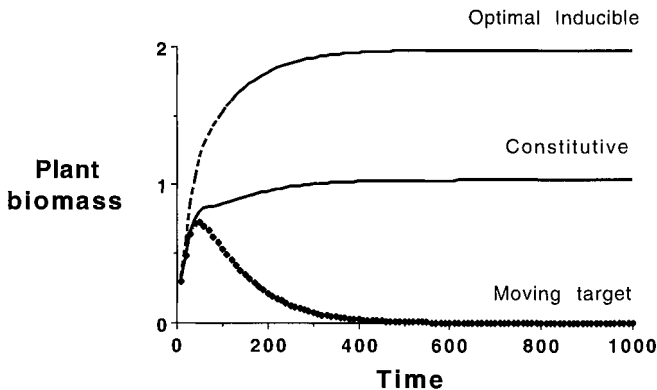


FIG. 2.—Results of competition among the constitutive strategy (*solid line*), the optimal inducible strategy (*dashed line*), and the moving target strategy (*dotted line*) when faced by a constant herbivore population. The values shown are the averages across states for each of the strategies as a function of time. Parameter values are $r_1 = 2.0$, $r_2 = 1.8$, $\bar{h}_1 = 1.0$, and $\bar{h}_2 = 1.0$. Other parameter values are as listed in the text.

target strategies in a temporally variable environment. Our goal is to describe the conditions favoring each of these strategies. In particular, we vary the number of herbivore species encountered, their average population densities, and the degree to which defenses reduce the density-independent growth rate.

For simplicity, we assume only two states ($n = 2$) and set state 1 to be more susceptible to attack by herbivores of type 1. In order to compete several species, the dynamics follow equation (1) with \bar{x} equal to the total biomass of all competing species. The lack of weighting in the sum means that each species and each state has identical effects on the other species. This obviates coexistence through competitive niche differentiation.

The dynamics of herbivory can be generated in several ways. First, and most fundamental for this article, the changes might be due to one or more than one type (species, population, age class, etc.) of herbivore. Second, as noted earlier, the dynamics of any given herbivore can have various degrees of coupling to the plant population. Herbivore numbers could be externally imposed stochastic or periodic functions of time, completely uncoupled from the status of the local plant population. In this case, actual herbivory rates (the e_i) might or might not be affected by plant populations because of foraging decisions by the herbivores. At the other extreme, herbivore numbers could be regulated by plant biomass or quality. Here we consider the first case, externally imposed stochastic dynamics without herbivore behavioral response to plant population characteristics. Models with partially and totally coupled herbivore dynamics are discussed in the Appendix.

Externally imposed stochastic herbivore dynamics could take many forms, ranging from fairly small fluctuations around an intermediate level to occasional outbreaks punctuating periods of very low herbivory. Outbreaks best describe the experience of a single plant and are considered here. In addition, the popula-

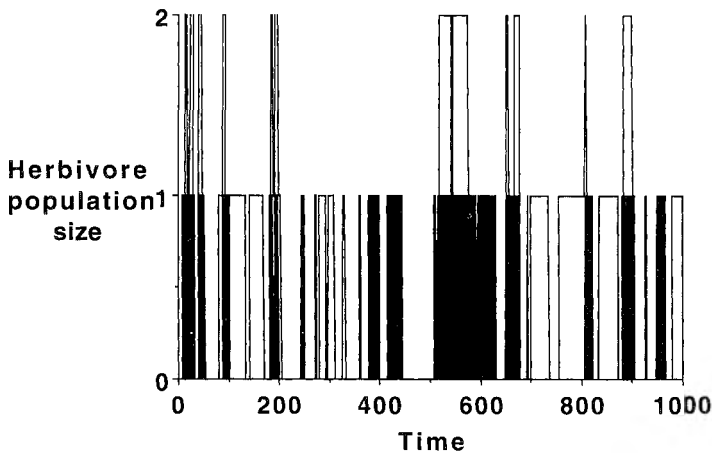


FIG. 3.—The herbivore dynamics used for the remaining simulations. The dark areas give the population size of herbivores of type 1, and the light areas give the population size of herbivores of type 2. Here $\bar{h}_1 = 1.0$ and $\bar{h}_2 = 1.0$.

tions of several herbivore species might or might not be correlated. In order to emphasize the uncertain conditions experienced by plants, we focus on the uncorrelated case. Figure 3 illustrates the dynamics of the two herbivores used in our simulations. The herbivore population levels during outbreaks (\bar{h}_1 and \bar{h}_2 for types 1 and 2, respectively) are used as free parameters. The trajectories were generated by a simple Markovian process: in each time step, a herbivore with population of zero has a 0.03 probability of beginning an outbreak, and an outbreak has a probability of 0.05 of ending in a given time step. On the average, there are 33 time steps between outbreaks that average 20 time steps in length. The outbreaks of the two species are completely independent of each other, of total plant biomass and state distribution, and of the past.

The parameters used in the simulations are presented as follows: $n = 2$, $r_1 = 1.8$ – 2.0 , $r_2 = 1.8$ – 2.0 , $a_1 = 1.0$, $a_2 = 1.0$, $m = 2$, $\bar{h}_1 = 1.0$, and $\bar{h}_2 = 0.0$ – 1.0 . We assume that the matrix k_{ji} of herbivore consumption ability is

$$\begin{pmatrix} 1.0 & 0.5 \\ 0.5 & 1.0 \end{pmatrix}. \quad (6)$$

That is, each type of herbivore is most damaging to a particular plant state and is only half as damaging to the other. Such a trade-off is essential in obtaining the results. The same plant states and herbivore effects are used for each of the three strategies.

Figure 4 presents the results when the three plant species are faced by a single herbivore type (the first type in fig. 3). We assume a high cost (10% reduction in growth rate) for state 2, which is 50% defended against herbivores of type 1. Recall that the optimal inducible strategy was designed precisely to deal with this situation. As expected, this strategy decisively dominates the other two in competition.

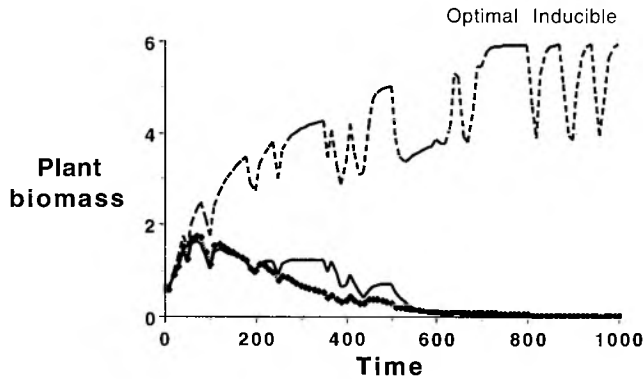


FIG. 4.—Competition among the three strategies when faced by a single herbivore ($m = 1$). Parameter values are $r_1 = 2.0$, $r_2 = 1.8$, and $\bar{h}_1 = 1.0$.

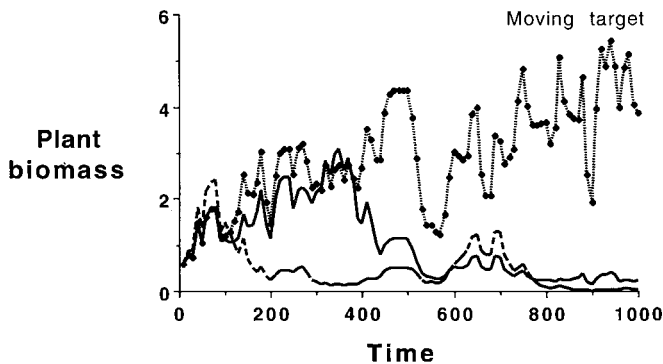


FIG. 5.—Competition among the three strategies when faced by two species of herbivores with no reduction in growth rate for state 2 plants. Parameter values are $r_1 = r_2 = 2.0$, $\bar{h}_1 = 1.0$, and $\bar{h}_2 = 1.0$.

The dynamics in the herbivory environment for which the moving target was designed are illustrated in figure 5. There are now two herbivore types with equal population sizes (as illustrated in fig. 3), and the two plant states have identical growth rates. As expected, the moving target strategy comes out on top in competition. The optimal inducible strategy is penalized during outbreaks of the second herbivore type, because by switching in a predictable direction it actually switches to the more vulnerable state 2.

In the same environment as figure 5, but with a sufficiently high cost of defense (low growth rate in state 2), state 1 is superior, and a constitutive state of no defense is favored (fig. 6). Both the moving target and optimal inducible strategies switch out of state 1 to the slow-growing state 2 when attacked. The moving target does so on principle, as it were. The optimal inducible strategy does so when it "misinterprets" a moderate level of attack by herbivores of type 2 as a huge attack by herbivores of type 1 and mistakenly "seeks" safe haven in state 2.

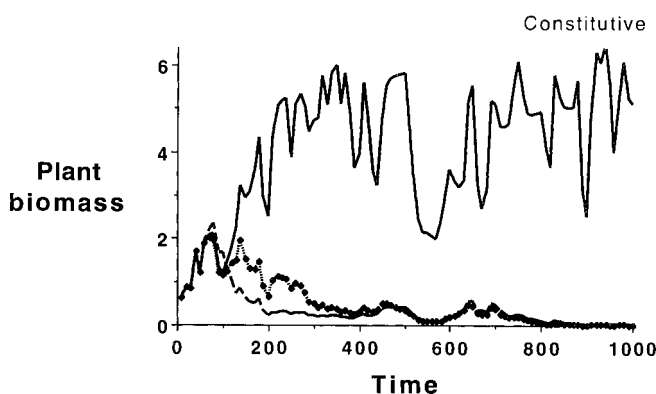


FIG. 6.—Competition among the three strategies when faced by two species of herbivores with a large reduction in growth rate for state 2 plants. Parameter values are $r_1 = 2.0$, $r_2 = 1.8$, $\bar{h}_1 = 1.0$, and $\bar{h}_2 = 1.0$.

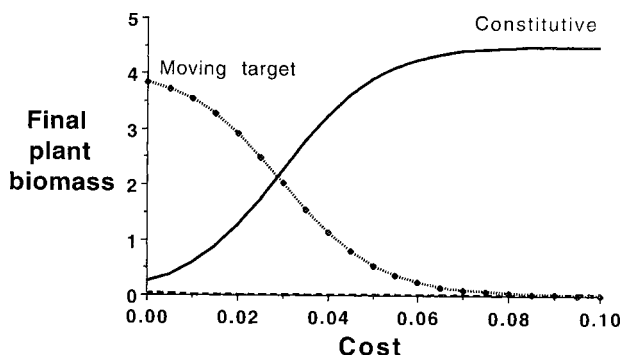


FIG. 7.—The biomass of plants expressing each of the three strategies after 1,000 time steps of competition as a function of the cost of defense measured as the percentage by which r_1 exceeds r_2 . Here, $r_1 = 2.0$, $\bar{h}_1 = 1.0$, and $\bar{h}_2 = 1.0$.

Figure 7 shows the biomass of the three types after 1,000 time steps of competition as a function of the cost of defense in the same environment as figure 6. The lines connect the cost-free case, which favors the moving target strategy, to the high-cost case, which favors the constitutive strategy. In all cases, the optimal inducible strategy does poorly because of the high population size of herbivores of type 2. If such simulations were run for a sufficiently long time, there would be no coexistence of strategies but a sharp switch between the moving target and constitutive strategies at some intermediate cost. This figure illustrates the relative competitive success of the strategies over the medium term.

Figure 8 shows a transect between the conditions most favorable to the optimal inducible strategy to those favorable to the moving target and constitutive strategies. The population of herbivores of type 2, to which the optimal inducible type responds inappropriately, is increased from 0.0 (as in fig. 4) to 1.0 (equal to the

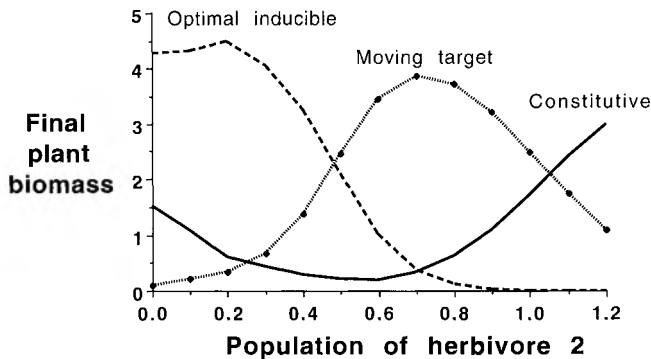


FIG. 8.—The biomass of plants expressing each of the three strategies after 1,000 time steps of competition as a function of the size of outbreaks of herbivores of type 2 (\bar{h}_2). Parameter values are $r_1 = 2.0$, $r_2 = 1.95$, and $\bar{h}_1 = 1.0$.

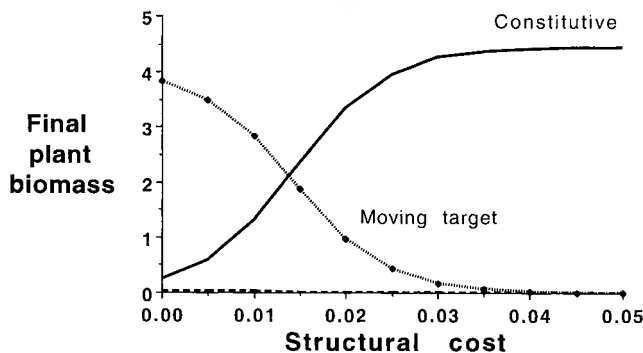


FIG. 9.—Competition among the three strategies when faced by two species of herbivores with no reduction in growth rate for state 2 plants but with a range of structural costs for the optimal inducible and the moving target strategies. The costs are measured as the percentage reduction of both r_1 and r_2 from their value of 2.0 for the constitutive strategy. As in fig. 5, $\bar{h}_1 = 1.0$ and $\bar{h}_2 = 1.0$.

population of the first type, as in fig. 5). Considered here is a low-cost scenario, with the growth rate of the undefended type exceeding that of the defended type by 2.5%. Note that the constitutive type makes a comeback as the population of type 2 herbivores increases, just as in figure 6. This is due to the developing intrinsic superiority of state 1 and the maladaptive effects of switching to the dangerous and costly type 2.

Many discussions of the costs of inducible defenses have focused not on the relative costs of different states but on the absolute cost of having the machinery to switch at all. As long as costs are not too high, however, the success of the inducible strategies in competition is maintained (Seger 1992). Figure 9 shows results based on the situation depicted in figure 5 in which the moving target strategy won in the absence of costs. We here assume that a structural cost deducts the given percentage from the growth rate of the optimal inducible strat-

egy and the moving target strategy in each state. When such structural costs become sufficiently large, the constitutive strategy dominates. However, when costs are not too large, the moving target maintains the superiority it has with no structural costs. Similar results can be obtained in situations (such as that shown in fig. 4) in which the optimal inducible strategy is favored.

DISCUSSION

Each of the three strategies is favored under some set of conditions. When populations of herbivores are constant, the constitutive and optimal inducible strategies outcompete the moving target strategy (fig. 2). With a single species of herbivore and a costly defense, the optimal inducible strategy is favored (fig. 4). When two species of herbivores are present that are differentially affected by the plant's defenses, the best strategy depends on the cost of defense and the relative populations of the herbivores (figs. 7, 8). If an inducible strategy is optimized with respect to one herbivore and the population of another herbivore, to which it responds inappropriately, is high, the optimal inducible strategy is eliminated (figs. 6, 7). The moving target strategy is favored when costs of defense against the first herbivore are low, and the constitutive strategy is favored when costs are so high that defense against the first herbivore is not worthwhile (fig. 7). If costs are intermediate, the optimal inducible strategy is favored when the population of herbivores to which it responds inappropriately is small (fig. 8). As that population increases, the moving target strategy is favored as before. Finally, a sufficiently large structural cost to maintain the capacity for induction can eliminate the superiority of the moving target strategy, but the strategy can be maintained even with a significant structural cost (fig. 9).

Figure 8 illustrates the potential effects of long-term herbivore dynamics on the evolution of these strategies. An exquisitely evolved, even optimal, inducible response to a particular herbivore can be undercut by the gradual appearance of an unfamiliar herbivore against which a particular defense is inappropriate. Such a herbivore might simply invade, or might evolve, perhaps even to exploit the predictable responses of inducible plants. If the plant could distinguish the attacks of the two herbivore types, it could evolve a sophisticated and appropriate response to the attack, but this strategy could be undercut by the appearance of a third strategy or modification of one of the existing herbivores. Only if the herbivore community were highly stable over long periods of time could a finely tuned optimal inducible strategy be expected to evolve (in the absence of a phenotypically responsive and precise mechanism like the vertebrate immune system). The success of an inducible strategy requires that the environment be information rich. If the environment has a tendency to evolve to break down information, through evolution of herbivores to capitalize on the errors of the plants or through the noise of individual experience, only a strategy like the moving target can be robust. The moving target strategy uses only the cue of damage itself, which is difficult to conceal in even the most information-poor environment. Although the moving target strategy is never the best response to a given environment, it is robust to unknown fluctuations in that environment.

Induced resistance will be favored over constitutive resistance because it allows the plant to deal with unpredictability. A moving target strategy is favored when the environment is both unpredictable and uninformative. Herbivory environments that change significantly over ecological time may not allow for the evolutionary fine-tuning required for a complicated, specific inducible response. The moving target strategy is the "poor plant's" version of the immune system, responsive to insults but incapable of identifying them. Such a response in some sense gives the herbivores a taste of their own medicine, by making a plant's current state maximally uninformative about the plant's future state.

Rausher et al. (1993) describe a dichotomy of views regarding induced resistance, contrasting broad-spectrum defensive responses most effective against generalists (the "diffuse" view) with a set of "distinct resistance mechanisms specific to different enemies" (the pairwise view). Our model contains elements of both, describing a multifaceted plant response to a diffuse community of herbivores. Instead of a single defense against that community or a set of single defenses against individual members of that community, we are proposing a diversity of defense, effective precisely because the plants are faced by a diverse community and can capitalize on negative correlations between the preferences and abilities of different herbivores.

More generally, our model shares elements with models of bet hedging, phenotypic plasticity, and coevolution. Bet-hedging models (Seeger and Brockmann 1987; Philippi and Seeger 1989) demonstrate that in a temporally variable environment with multiplicative fitnesses, genotypes can benefit from producing a range of phenotypes. Because the models in this article compare growth rates, which are additive rather than multiplicative, simple bet hedging is not favored. In phenotypic plasticity models, organisms choose their phenotype based on a cue containing some information about the environment (Adler and Harvell 1990). In this case, even with additive fitnesses and a marginally reliable cue, phenotypic polymorphism can be favored (Moran 1992). In models of exploiter-victim coevolution, exploiters evolve the ability to overcome resistance. The dynamics can maintain defensive polymorphism when there is matching between specific exploiter and victim phenotypes (Levin et al. 1977; Seeger 1992; Hori 1993). The moving target model requires the existence of such matching to maintain the reliability of the cue, but the preservation of phenotypic diversity does not depend on the tightly linked dynamics typical of coevolution models.

Our model makes predictions about the conditions that favor induced defenses and constitutive defenses. There are now literally hundreds of plant-herbivore systems in which empiricists have looked for evidence of induced resistance, and these should allow testing of the predictions of these models. The moving target model predicts that the amount of variability in phenotypic states over time (which can be estimated empirically), rather than the identity of the actual states, should be correlated with resistance. By comparison, the optimal inducible model predicts that there should be more and less defended states and that the defense level should be correlated with resistance and with costs. Testing the effects of a particular phenotypic change on a single herbivore is not sufficient to distinguish the different inducible strategies. Rather, tests of multiple induced plants faced

by multiple herbivores are required, in concert, ideally, with detailed multitrait descriptions of the induced response. Restricting experiments to one dimension at a time can restrict thinking to one dimension, which is inappropriate even for plants.

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APPENDIX

A TIGHTLY COUPLED MODEL

We first present a model of eating rates coupled to herbivory through herbivore behavioral responses to plant characteristics. We then show how behavior can be included in a tightly coupled model of plant-herbivore dynamics in which plants and herbivores mutually control the populations of the others.

Recall that equation (1) requires computation of the eating rate e_i from plant and herbivore population distributions. Equation (2) ignores herbivore behavior in making this calculation. We here develop a submodel of herbivore foraging and feeding behavior. The herbivores follow a simple foraging rule; a herbivore of a given type (l) remains on a plant in a given state (i) for a duration τ , which is a function of the herbivore's ability to consume the plant (k_{li}). The function τ gives the preference of herbivores for plants that they are more successful at consuming, with a natural functional form being

$$\tau(k_{li}) = k_{li}^\rho, \quad (\text{A1})$$

where ρ is the preference. When $\rho = 0$, there is no preference. The search time between successive feeding bouts is a function of the herbivore's intrinsic searching ability and the total biomass of plants. We assume that the herbivores redistribute themselves on plants at a rate fast relative to that of their population dynamics.

The variables used in this submodel are as follows: h_{li} , number of herbivores of type l per unit in state i ; $\tau(k_{li})$, residence time of herbivores of type l on plants in state i ; S_l , number of searching herbivores of type l ; c_s , searching ability of herbivores of type l ; \hat{x}_i , total biomass of plants in state i ; f_i , food available to herbivores of type l ; and μ_l , mortality rate of herbivores of type l . We set h_{li} to be the number of type l herbivores per unit of plant in state i and let S_l denote the number of searching herbivores of type l . Because all herbivores must either be on a plant or searching, we have

$$\sum_{i=1}^n h_{li} \hat{x}_i + S_l = h_l. \quad (\text{A2})$$

The total number of type l herbivores on state i plants is $h_{li} \hat{x}_i$ because h_{li} is defined per unit biomass. Then

$$\frac{d}{dt} (h_{li} \hat{x}_i) = c_s S_l \hat{x}_i - \frac{h_{li} \hat{x}_i}{\tau(k_{li})}. \quad (\text{A3})$$

The first term represents discovery of plants of state i by searching herbivores, assumed to occur by random encounter. The second term gives the rate at which herbivores leave to enter the searching pool and is inversely proportional to the residency time. If the herbivores redistribute quickly, one can assume that the process remains near equilibrium (the quasi-steady-state approximation), and equation (A3) can be set equal to zero and solved, which gives

$$h_{li} = c_s S_l \tau(k_{li}). \quad (\text{A4})$$

Substituting this expression into equation (A2), we find that

$$\begin{aligned} S_l &= \frac{h_l}{1 + c_s G_l} \\ h_{li} &= \frac{c_s \tau(k_{li}) h_l}{1 + c_s G_l}, \end{aligned} \quad (\text{A5})$$

where

$$G_l = \sum_{i=1}^n \tau(k_{li}) \hat{x}_i.$$

We can then compute e_i as

$$e_i = \sum_{l=1}^n h_{li} k_{li}. \quad (\text{A6})$$

The eating rate experienced per unit of plant in state i is the sum over all herbivores of the number of herbivores per unit plant times the eating efficiency.

Using equation (A6) rather than the simple equation (2) to compute the eating rates used in model 1 constitutes a partially coupled model in that the herbivores respond behaviorally but not numerically to the characteristics of the plant population. The same reasoning used to derive equation (4) can be used to find the optimal inducible response in this case, modified in that preferences alter the distribution of herbivores. Except for scaling considerations (the average efficiency of herbivores is reduced by including search time), the results from the partially coupled model closely match those of the uncoupled model. This holds for values of the preference ρ (eq. [A1]) ranging from zero (no preference) to four (intense preference).

Having computed the distribution of time spent by herbivores on plants in different states, we are able to compute the food intake f_l of a herbivore of type l as

$$f_l = \sum_{i=1}^n h_{li} \hat{x}_i k_{li}. \quad (\text{A7})$$

The food intake by type l herbivores is the sum over all plant states of the total number of herbivores on plants in that state times the eating efficiency.

This eating success can be used to create a totally coupled model of plant-herbivore dynamics. In particular, we can set

$$\frac{dh_l}{dt} = \beta_l f_l - \mu_l h_l, \quad (\text{A8})$$

where μ_l is the mortality of herbivores of type l . The potential costs of the capability of consuming defended plants can be absorbed into the mortality μ . The equation describing the dynamics of the plants is once again equation (1).

The behavior of this model is substantially more complicated than the earlier models.

The analysis of the case with constant herbivory levels still applies, however, so that stable dynamics never favor switching. However, like the predator-prey models that it resembles, this totally coupled model has a tendency to oscillate, and the oscillations are capable of supporting the moving target strategy. Unlike the models with externally imposed herbivore dynamics, this model is capable of supporting coexistence of various plant strategies. We feel that these results are less robust for the situation under consideration than those presented in the main text.

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